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The Role of Interactions between Bacteria and Clay Minerals in Pedochemical Processes

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Abstract—The paper reviews bilateral interactions between bacteria and clay minerals and their effect on the chemical composition of soils and chemical processes in them. Bacteria are demonstrated to be involved in weathering processes and in transformations and synthesis of clay minerals and thus change water-retaining properties of the soils, maintain their fertility, and contribute to the cycling of nutrients and contaminants. The paper describes diverse processes of direct and indirect effects of phyllosilicates on the microbiological activity and microbial diversity in soils, as well as the biogeochemical role of these processes. The wide occurrence of the various types of interactions between bacteria and clay minerals is obviously controlled by the First Biogeochemical Principle formulated by V.I. Vernadsky.

Keywords: microorganisms, immobilization of bacteria on clays, biological weathering, transformations and synthesis of clay minerals, environment-forming role of phyllosilicates

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INTRODUCTION

The various objects and systems of the biosphere are affected by and involved in common biospheric processes. During the evolution of our planet and life on it, living and inert matter evolved simultaneously, interacted, and not only modified one another but also operated together to form still another type of matter: bio-inert. Bio-inert material is both a product and a new environment, in which physical, chemical, physicochemical, and biological processes proceed that are typical exclusively of this environment. "Bio-inert natural bodies are typical of the biosphere. These are systematic structures that consist of inert and living bodies (for example, soils), and all of their physicochemical properties require fundamental corrections (sometimes very significant) if living matter was disregarded when they are studied" (Vernadsky, 1980).

In his paper "On the Participation of Living Matter in the Formation of Soils", V.I. Vernadsky discussed the role of living matter in processes that control the composition and properties of soils (Vernadsky, 1992). He understood living matter as "...all organisms (plants and animals, including humans) considered collectively". Nevertheless, the types of effects of living organisms on soil-forming processes are also fully typical of microorganisms. Moreover, such processes also occurred during the early evolution of the biosphere, when the trophic structure of ecosystems consisted only of prokaryotes. V.I. Vernadsky distinguished the following types of the effects:

"Living matter functions through its mass and the composition of its material. Living matter *per se* is a component of soils either by itself or in the form of its transformation products and as dying away and/or dead living matter.

Living matter is responsible for the stone-free character of soils.

Living matter modifies the structure of soils through the loosening or cementing activities of the living organisms or products of their dying-away.

Living matter immediately affects chemical processes in soils, is a leading factor of this mixing, and thus controls the proceeding of all chemical reactions in soils.

Living matter introduces foreign material from far away into soils and thus disturbs the ratios of soils and subsoils by acting by itself through its mass or indirectly affecting this process" (Vernadsky, 1992).

So, properties and functions of natural and anthropogenic bio-inert systems (soils, grounds, silts, biofilms, etc.) are thus controlled by living matter and its diverse and complex interactions with the environment, as well as products of these interactions. A special role in bio-inert systems is played by microorganisms, including bacteria, because they are the most widely spread type of living matter and have lived on the planet much longer than larger life forms, with much bacteria continuously living in immediate contact with mineral surfaces (Cuadros, 2017). Clay minerals (layered aluminosilicates) are the most widely

spread minerals of weathering crusts and soils. Their high specific surface makes these minerals one of the reactive surfaces in soils. Keen interest is provoked by interactions between phyllosilicates and bacteria and by the effects of these interactions on pedochemical processes. These interactions are very diverse (e.g., Stotzky, 1986; Cuadros, 2017; Li et al., 2019; Fomina and Skorochod, 2020), but obviously not all of them are widespread and are important for the biosphere as a whole.

Interactions between bacteria and clay minerals are of mutual nature. Microorganisms significantly affect minerals and modify their surface by being involved in, on the one hand, weathering and, on the other, in the precipitation and crystallization of newly formed minerals (Konhauser and Urrutia, 1999). Minerals can, in turn, affect microbiological activity both directly and indirectly (Stotzky, 1986): directly, i.e., by immediately physically affecting the surface of minerals and microorganisms; and indirectly through modifying the microhabitat of the microorganisms. The changes in the habitat may include maintaining an optimum level of humidity, contents of nutrients, and pH (Novitzky, 1986; van Loosdrecht et al., 1990), adsorption of toxic microbial metabolites and contaminants, which can adversely affect vital functions of the microorganisms (Stotzky, 1986). Lately more and more attention is attracted to mechanisms of these interactions in the context of the development of new technologies based on these mechanisms, such as microbiological purification of clay minerals, their synthesis and recycling, the utilization of clays for adsorption and/or removal of organic and/or inorganic contaminants from soils, etc. (Li et al., 2019; Perelomov et al., 2021). Below we discuss various aspects of interactions between bacteria and clay minerals in the context of their influence on chemical processes in soil systems, more specifically, on the elementary soil chemical processes according to (Zakharov, 1927) or soil-forming microprocesses in the terminology in (Rode, 2008).

IMMOBILIZATION OF BACTERIA ON CLAY MINERALS

About 90% bacteria occur in nature in the form of biofilms at different stages of their development (Dalton and March, 1998). A biofilm is a structurally organized community of microorganisms that occurs within a polymer matrix, which was synthesized by members of the community, and is attached to any surface (of mineral, organic, or biological nature) (Il'ina and Romanova, 2021). An empirically established fact is that bacteria prefer to live attached to an available surface instead of in ambient aqueous phase as plankton. Although this fact is obvious, the fine mechanisms of the attachment of microorganisms to mineral surfaces are still understood inadequately poorly.

Planktonic microbial cells are first transferred from the liquid volume into the near-surface layer of the liquid (this layer is conditioned by the surface and is a boundary layer) either by physical forces (such as Brownian agitation, Van der Waals forces, gravity forces, influence of the surface electrostatic charge and hydrophobic interactions, etc.) (Gottenbos et al., 2000) or by bacterial structures, such as flagella. A certain contribution to this transfer may also be made by chemotaxis and haptotaxis (Kirov, 2003). The surface of clay minerals is able to adsorb both nutrients and toxicants. Stotzky (1986) pointed out that a mineral surface does not distinguish between adsorbates that are "good" or "bad" for microorganisms. Because of this, chemotaxis likely does not play any significant part in the immobilization of bacteria. Upon reaching the surface, cells can reversibly attach themselves to it. Numerous parameters of properties of the surface, near-surface environment, and the bacterial film (such as available energy, the occurrence of functional groups, charge, surface geometry, temperature, pressure, etc.) are local variables on which bacterial adhesion depends (Garret et al., 2008).

Physicochemical interactions between microorganisms and the surface of soil particles are conventionally described within the framework of the Deryagin–Landau–Verway–Overbeck (DLVO) theory, which provides a theoretical basis for understanding the aggregative stability of dispersed systems. In its classic variant, this theory deals with the process of coagulation as a result of interplay of the Van der Waals (dispersion) attraction forces and electrostatic repulsive forces between the particles. Depending on the balance of these forces in the thin liquid layer between the mutually approaching bodies, either positive "disjoining" pressure emerges, which hinders their convergence, or negative pressure develops, which thins the liquid layer and brings the particles into mutual contact (Deryagin and Landau, 1941; Verwey, 1947). The DLVO theory considers the possibility of aggregation of particles at both short distances, with bridging the potential repulsion barrier, and at long ones, with crossing liquid layers (Fig. 1).

The modern extended theory of aggregative stability (extended DLVO theory) involves not only molecular and electrostatic but also other components of repulsion forces. The extended DLVO theory makes it possible to evaluate the interaction energy of particles with regard to molecular, electrostatic, adsorption, and structural components of disjoining pressure (Chang and Chang, 2002; Gallardo-Moreno et al., 2002). The classic and extended DLVO theories identify energy barriers that should be overcome by a cell when it attaches itself to a surface from solution (coagulation), but the mechanisms of this overcoming remain unknown, particularly when negatively charged clay minerals interact with bacterial films that are also negatively charged.

The attachment of cells to a mineral surface may be complicated and involve several stages. For example,

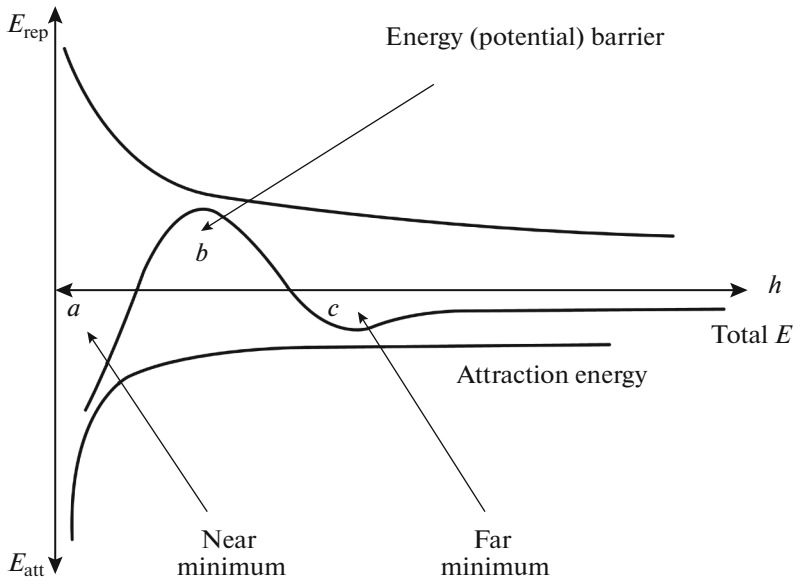

Fig. 1. Dependence of the bilateral interaction energy of particles on the distance between them (modified after Molodkina, 2010). Segments: (a) near energy minimum (at short distances of about 100 nm) with the predominance of attraction forces; (b) potential repulsion barrier, energy maximum, with the predominance of Coulomb repulsion forces, with the height of the barrier depending on the surface charge and the thickness of the diffuse layer; (c) far energy minimum (at relatively large distances of about 1000 nm), with the predominance of attraction forces).

An and Friedman (1998) argued that the process of bacterial adhesion consists of two phases and involves an initial phase of physicochemical interaction (reversible) and a later phase, which is molecular and cellular (irreversible). During the later adhesion stage, molecule-specific reactions between bacterial surface structures and substrate surface become dominant. This implies that bacteria are faster attached to the surface via selective binding with bacterial surface structures, which include capsules, pili, and mucus. If the substrate is host tissues, adhesines may operate as a functional part of these structures (Katsikogianni and Missirlis, 2004). It is believed that surface structures of microorganisms overcome the physical repulsion forces of the double electric layer (De Weger et al., 1987). Later on, the appendages of the cells come into contact with the volume of the conditioned surface layer, stimulate chemical reactions, such as oxidation and hydration (Ganesh and Anand, 1998), and strengthen bonds between the bacteria and surface. Some data indicate that microbial adhesion strongly depends on the hydrophobic–hydrophilic properties of the interacting surfaces (Liu et al., 2004).

An experimental study of the immobilization of cells of the bacterium *Paraburkholderia phytofirmans* on the surfaces of silicon dioxide, bentonite, and talc has shown that the adhesion of the microorganisms depends on pH and decreases as pH is increased from 5.5 to 9. The charge of the carrier surface also affects, although relatively insignificantly, the immobilization of bacteria. The amount of Mg^{2+} in the minerals was a key parameter controlling the degree of cell immobilization (talc > bentonite > silica). The greatest amount of bacterial cells were found on talc, which is the most hydrophobic mineral among the tested ones. A similar immobilization capacity was identified for all of the three minerals if the bacteria were cultivated and adsorbed simultaneously. This may be explained by that a biofilm at its cultivation is formed via the clonal growth of the primarily attached bacteria but not via recruiting planktonic cells (Bejarano et al., 2017).

After reversible and irreversible adhesion (fixation), microcolonies are formed, which are separate accumulations of attached microorganism cells (Fig. 2).

The microorganisms actively proliferate during this stage, and the matrix keeps the colony together (maturation stage I). When growing, the colonies merge and thus form a mature biofilm of complex 3D structure and a common extracellular matrix, which has a stable inner environment and protects the colony from adverse external factors (maturation stage II). The matrix may serve for the attachment of other microorganisms and as a nucleus on which new minerals are formed. Upon the exhaustion of resources within the biofilm, the microorganisms may leave it and pass into a planktonic form (dispersion stage). During this stage, single cells periodically disconnect themselves from the film and are in a while able to attach themselves to a surface and start to form a new colony (Fig. 2) (Palanisamy et al., 2014; Karaguler et al., 2017). In fact, a biofilm is the minimal bio-inert system, and the simplest biogeochemical processes proceed at this level.

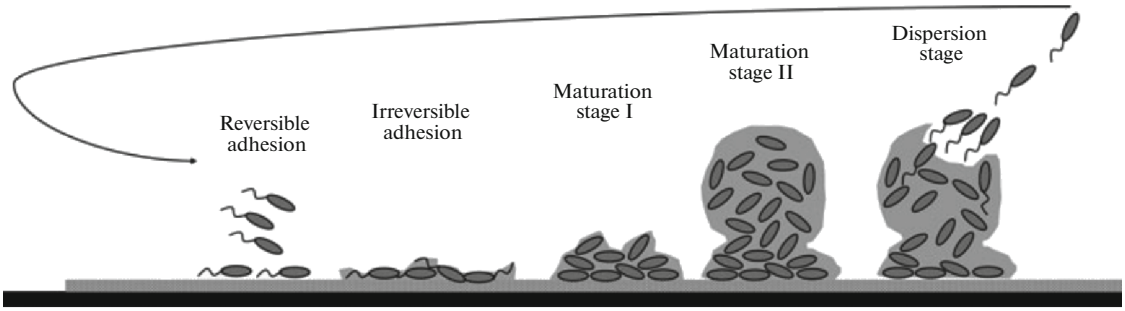

Fig. 2. Stages of the origin and evolution of a biofilm (modified after Palanisamy et al., 2014).

EFFECT OF BACTERIA ON CLAY MINERALS

Much attention is lately attracted to the various aspects of the involvement of microorganisms in alterations of clay minerals, such as their aggregation, weathering, and transformations, in which the phyllosilicates undergo significant transformations: their structure, specific surface area, basal spacing, composition of exchange cations, cation exchange capacity, etc are modified. This affects chemical and physicochemical properties of the soils (Maurice et al., 2001; Mueller, 2015; Li et al., 2019; Fomina and Skorochod, 2020).

In soils and weathering crusts, microorganisms play a fundamental role in destructing and decomposing phyllosilicates and thus increase the porosity of the soils and their permeability to water, maintain their fertility and a high quality of the surface waters, and contribute to the cycling of nutrients and contaminants (Mueller, 2015). Biodegradation was identified for such minerals as kaolinite, halloysite, illite, montmorillonite, vermiculite, serpentine, chrysolite, etc. Various clays are differently resistant to biological destruction. Dioctahedral clay minerals (kaolinite, halloysite, illite, montmorillonite, and some others) are thought to be more resistant than trioctahedral phyllosilicates (vermiculite, serpentine, chrysolite, etc.). Chlorites show an intermediate resistance (Dobrovol'skii et al., 2003).

The weathering of clay minerals under the effect of microorganisms proceeds by means of processes of the following two major groups: biomechanical and biochemical, which are also typical of the microbial weathering of other minerals and rocks (Gadd et al., 2007; Fomina and Skorochod, 2020). In biomechanical processes, microbial cells either directly interact with the mineral surface or indirectly affect them with the involvement of microbial products, including exopolymers. The swelling or contraction of cells, their metabolic products, and biofilms activate bioerosion and bioabrasion (Gaylarde and Gaylarde, 2004).

Biochemical processes are more efficient in destroying clays (Kumar and Kumar, 1999; Fomina and Skorochod, 2020). Heterotrophic organisms (bacteria and microfungi) dissolve phyllosilicates in the course of so-called heterotrophic leaching (or chemoorganotrophic leaching), a process that involves two stages: acidolysis and complexolysis (Sand and Bock, 1991). These mechanisms may be associated with redoxolysis: a change in the redox potential of the medium under the effect of bacteria and ensuing changes in the extraction and mobility of metals contained in phyllosilicates. The oxidation and reduction of elements of variable valence may proceed under the effect of both auto- and heterotrophic microorganisms.

Acidolysis or proton-stimulated dissolution occurs when microorganisms acidify the environment by releasing protons and organic acids, and carbonic acid is formed from metabolic carbon dioxide (Burgstaller and Schinner, 1993).

Many microorganisms are able to release metabolites that form complexes with metals and induce ligand-stimulated dissolution or complexolysis of phyllosilicates. Complexing agents of this type are carboxylic acids, aminoacids, Fe(III)-binding siderophores, phenol compounds, etc. (Gadd, 2010). Carboxylic acids (for example, oxalic and citric acids) are sources of both complexing ligands for metal ions, including Al and Fe, and protons for the solubilization of clays (Dong, 2012). Both of these processes were clearly demonstrated in the experiment (Liu et al., 2006). The silicate bacterium *Bacillus mucilaginosus* dissolved mica and simultaneously released K^+ and SiO_2 from the crystal lattice, but no feldspar was thereby dissolved. During its growth, *B. mucilaginosus* produced polysaccharides and attached themselves to the mineral surface, which resulted in a domain with a high concentration carboxylic acids near the mineral. The polysaccharides consumed silicon, and this modified the equilibrium between the mineral and liquid phases and induced solubilization reactions of K and Si (Liu et al., 2006). Potassium is known to be principally important for the mineral nourishment of plants, and silicon compounds play a significant role in maintaining soil fertility (Bocharnikova et al., 2011). The liberation of much Al, and usually also Si, at the microbiological dissolution of kaolinite due to both pH changes by bacteria and their synthesis of an Al-

chelating agent was mentioned in (Maurice, 2001). The mechanisms of acidolysis and complexolysis operate at the destruction of clay minerals with an expanding structural cell, for example, smectite (Wu et al., 2008; Oulkadi et al., 2014). The extent of mineral dissolution depends on the nature and amounts of the microbial metabolites (H^+, OH^-, ligands, etc.) and the surface reactivity of the phyllosilicates (Grybos et al., 2011).

The metabolism of a specific group of chemolitotrophic bacteria (archaea and bacteria) may also be associated with the synthesis of strong mineral acids. For example, autotrophic nitrifier bacteria form nitric and nitrous acids, and sulfur bacteria produce sulfuric and sulfurous acids (Dobrovol'skii et al., 2003), which effectively participate in proton-stimulated acidolysis.

Another mechanism destructing clay minerals is redoxolysis (Ehrlich, 1996; Lloyd, 2003): microorganisms produce catalytic compounds that modify the redox potential of the solution and thus release metals and elements bound to them in the phyllosilicates. The efficiency of this destruction of minerals depends on characteristics of the mineral phase, on whether the metal is reduced/oxidized, and on its oxidation state (Mishra and Rhee, 2014). Iron ions are among the most widely spread redoxolysis agents, and Fe^{3+}, which can be produced under the effect of iron oxidizers, starts to act as an oxidizer for other metals, which leads to the dissolution of some compounds. The reoxidation of Fe^{2+} to Fe^{3+} makes the reaction cyclic (Schippers et al., 1996). Not only essential ions but also microorganisms themselves can oxidize elements of variable valence that are contained in silicate rocks and minerals (Dobrovol'skii et al., 2003), because reduced species of elements can provide energy for the bacteria when oxidized. This may result in the decomposition of aluminosilicates and the removal of structural and exchange metal cations and the breaking of siloxane and aluminum–oxygen bonds.

The processes of biological weathering of clay minerals often lead to transformations of these minerals and the formation of some minerals at the sacrifice of others or to the synthesis of newly formed phyllosilicates from the decomposition products. For example, it has been found out (Kompantseva et al., 2013) that bacteria can increase the cation-exchange capacity of kaolinite by notably modifying its crystal morphological characteristics. The kaolinite particles diminished and partly dissolved when interacting with bacteria, and the crystal structure of the mineral became ordered due to a decrease in the number of stacking faults of the layers of the lattice structure. Biodissolution affected first of all marginal portions of the mineral grains. The process of biodegradation affected not only crystal morphological features but also the mineralogy of the phyllosilicate samples: gibbsite was formed in the presence of bacteria, the mica component was partly decomposed, and a mineral-organic complex was formed (Kompantseva et al., 2013).

Now more than 100 minerals, including phyllosilicates, are known whose genesis may be related to activities of microorganisms (Astaf'eva et al., 2011; Fomina and Skorochod, 2020). Data acquired on some fossil bacteria indicate that mineral-forming processes that were induced by them, or process in which they were involved, was started on the planet when the bacteria themselves emerged on it, i.e., practically when modern life forms were formed (Samylina et al., 2002). Bacteria may be involved in all processes related to the origin and transformations of clay minerals and are able to significantly accelerate these processes (Neimark et al., 2009). It has been established that microorganisms and their organic metabolites participate in processes that form some clay minerals: kaolinite, smectite, chlorites, etc. (Rozanov, 2003). SEM studies of Carboniferous white clays in the Moscow region have shown that biogenic clays have bacteriomorphs that are obviously traces of filamentary cyanobacteria that surrounded coccoid bacteria (Astaf'eva and Rozanov, 2010).

The paper (Linares and Huertas, 1971) gives a powerful impulse to studying processes of biogenic forming phyllosilicates. These authors have described a process in which solution containing Si, Al, and peat fulvic acid precipitated kaolinite at room temperature. The authigenic precipitation of clay minerals in an aqueous environment rich in organic matter and in the presence of bacteria, which facilitate the decomposition of organic matter was described in much detail in (Konhauser et al., 1993). The authors have demonstrated that iron cations actively precipitate onto the surface of bacterial cells and then serve as loci for the origin and further growth of a fine-grained mineral phases of Fe–Al silicates of different composition, which range from the almost amorphous gel-like to crystalline. The composition of the gel structure is close to that of chamosite clay (Fe-rich chlorite), and the crystalline phase is of kaolinite composition. Chaerun et al. (2005) and Tazaki (2005) have demonstrated that microbe–mineral interactions can produce kaolinite and halloysite. Fiore et al. (2011) has proposed a scenario of a two-stage biologically induced process that forms kaolinite. During the first stage, aluminosilicate precipitates in the presence of oxalates and other organic compounds, including extracellular polymers that are metabolites of bacteria. Because of changes in the micromedium induced by the metabolic activity of the bacteria, the newly formed gel can locally dissolve or be transformed into a solid state with the simultaneous origin of kaolinite crystals. The deprotonation of amphoteric organic ligands in the polymers of the cell walls of the bacteria is negatively charged within a wide pH range. These ligands are binding with metal cations and operating as self-organization centers for kaolinite minerals (Pokrovsky et al., 2008; Liu et al., 2015). Kaolinite was

formed two month after iron-reducing bacteria (of the genus *Toxothrix* and *Gallionella*) were placed in contact with granite (Tazaki, 2005). Sulfur-reducing bacteria can operate as catalysts to form halloysite in soils (Herrmann et al., 2007). Kawano and Tomita (2001) pointed out that interaction of bacteria with Al and Si in old volcanic ash likely leads to the precipitation of allophane-like granulated minerals as a metastable phase in the pore water. The allophane-like materials can eventually be transformed into poorly ordered smectite-like fibers and/or flakes as an intermediate phase between allophane and nontronite. In liquids that contain Al and Si ions, beidellite-like smectite is formed bound to bacterial surfaces. At the same time, no minerals are formed in the same liquid if it does not contain either metals or bacteria (Kawano and Tomita, 2001). Processes forming clay minerals may involve organisms of the genus *Pseudomonas* (*Pseudomonas syringae*, *Pseudomonas fluorescens*), *Xanthomonas* (*Xanthomonas campestris*), *Shewanella* (*Shewanella putrefaciens* CN32), and some others (Mueller, 2015).

The processes described above show that geoactive microbes intensely participate in both the mobilization and the immobilization of metals: they can dissolve minerals (including clay ones), release mobile metal species and associated elements into the environment, and are also able to immobilize metals by means of their biosorption, transport, accommodation in cells, accumulation in living microorganisms (bioaccumulation) (Perelomov et al., 2013), redox immobilization, sedimentation, and biomineralization. This may lead to the formation of secondary biogenic minerals. These processes are of great ecological, economic, and social importance. Processes of microbial mobilization release nutrients (metals and associated elements) in forms bioavailable for plants and for other microorganisms in soils, as well as can form soils, grounds, and sediments as a consequence of weathering and destruction of rocks and minerals.

EFFECTS OF MINERALS ON BACTERIA

The biogeochemical activity of microbes in soils is inseparably related to effects of clay minerals on the growth of microbes and their metabolic activity. As was mentioned above, these effects can be both direct and indirect, and it is sometimes difficult to distinguish between these two types of the processes.

It is known that interactions between microbes and dispersed materials at certain concentrations may result in a layer of adsorbed mineral particles on the bacterial surfaces (Globa et al., 1983). The immobilization of small particles of clay minerals on the surface of bacteria and their biofilms protects them from drying and other adverse processes (Alimova et al., 2009). Also, attached clay particles may serve as loci for the accumulation of surplus amounts nutrients and water. At the same time, it has been demonstrated with the use of glauconite, saponite, and montmorillonite as illustrating examples that an increase in the content of mineral particles above a certain critical value suppresses the growth of bacteria (Kurdish and Bega, 2006; Chobotarov et al., 2010; Fomina and Skorochod, 2020). At a high content, the layer of adsorbed colloid particles operates as a barrier that hampers the uptake of nutrients and gases by the cells (Globa et al., 1983; Stotzky, 1986; Chobotarov et al., 2010).

The influence of phyllosilicates on microbial physiological and biochemical processes depends on the group of the microorganisms (archaea, bacteria, and fungi), varies from one species to another (Neimark et al., 2009), and also determined by the species of the clay mineral. It has been demonstrated that interaction between clays and microorganisms may change the production of the biomass and growth rate, disturb the synchronization of microbial development, the duration of the growth retardation phase when microbes are cultivated, the utilization efficiency of the substrates, breathing activity, production of enzymes and metabolites, etc. (Fomina and Skorochod, 2020). It has been demonstrated that montmorillonite can enhance microbial activity where kaolinite does not, perhaps, because montmorillonite swells and possesses a greater adsorption capacity. If present, montmorillonite increases the capacity of the material for organic and inorganic compounds and ability of pH buffering (Ransom et al., 1999). At the same time, Vieira and Melo (1995) have documented an increase in the microbial activity of *Pseudomonas fluorescens* in a biofilm in the presence of kaolinite. They observed thereby an increase in the biomass of the bacteria and their breathing coefficient, the biofilms were more stable, and the mass transfer through them became more active.

It is quite commonly thought that clay minerals, which have high adsorption capacity, can concentrate organic compounds on their surface, where concentrations of these compounds reach levels high enough to support the growth of microbes. However, proponents of an alternative viewpoint, presented in numerous publications, claim that nutrients on the surface of clay minerals did not maintain the growth of microorganisms in the absence of an exogenic matrix. For example, montmorillonite, attapulgite (palygorskite), and kaolinite samples containing organic carbon and nitrogen did not affect the growth of microorganisms (Stotzky, 1986). When various organic growth media (such as proteins, peptides, aminoacids, polysaccharides, nucleic acids, and nucleotides) were adsorbed by clay minerals, their availability for microbes was usually lower (Stotzky, 1986). Hence, even if the surface of clay minerals in a soil is enriched in nutrients, these nutrients may be potentially unavailable for maintaining the vital functions of the microorganisms.

Some researchers have found out that clay minerals (for example, kaolinite) and rocks rich in clay minerals

(for example, bentonite) with high Al concentrations inhibit the growth of several bacteria (*Escherichia coli*, *Pseudomonas*, and *Desulfovibrio vulgaris*) and organisms of other genus (Fomina and Skorochod, 2020). Moreover, unlike growth media used in laboratory experiments with microorganisms, clay minerals in soil systems may concentrate on their surface organic compounds with a biocidal effect (Pasket et al., 2022).

Particles of clay minerals are small, and their specific surface area is great. The inner and outer surface area of phyllosilicates is hydrophilic and polar, and this facilitates wetting and interactions between their surface and low- and high-molecular organic compounds containing polar groups. At the same time, the polarity of the surface of silicates hampers interaction between montmorillonite and nonpolar and low-polarity compounds (Perelomov et al., 2021). Nevertheless, phyllosilicate particles in soils are always covered with organic films and form organo-mineral structures (Zubkova and Karpachevskii, 2001). It is believed that such aggregates may operate as swells of the biofilms and retain organic and inorganic nutrients on their surface (Fomina and Skorochod, 2020). However, given the originally hydrophilic character of the surface of clays, the development of such films that include much hydrophobic fragments may be caused by the activities of microorganisms and their biofilms immobilized on the clays. Thus, the matrix effect of soils when specific organic compounds are formed (Zubkova and Karpachevskii, 2001) and features of the biogeochemical cycling of chemical elements may be caused not only by mineral but also biological matrices. A matrix in soil is the surface of solid particles that organizes compounds around itself according to a certain pattern, in compliance with the properties of the surface of the particles. Interactions between microorganisms and clays may not only be mediated by organic matter, but also *vise versa*, interactions between organic matter with the surfaces of clay minerals may be controlled by microorganisms. Therewith the microbiological immobilization of organic matter on minerals may partly modify the character of the surface of the clays from hydrophilic to hydrophobic and facilitate the adsorption of other organic molecules. The strong fixation of organic molecules precludes their transfer and mineralization, and this is extremely important for the origin of humus.

The mineral nutrition of bacteria requires metals: macronutrients and essential trace elements. The quantitative demand in them corresponds to the sequence K > Na > Mg > Ca > Fe >> Mn, Co, Zn, Cu, Ni and Mo (Cuadros, 2017). Clay minerals are an important source of inorganic cations for bacteria. These cations can be released from minerals in the process of ion exchange, most commonly with protons that are liberated in the course of cell metabolism (Stotzky, 1986; Chobotarov et al., 2010). In addition, metal cations are released at the decomposition of phyllosilicates by bacteria in the aforementioned processes. Since minerals are variably resistant to biological weathering, bacteria should "apply" different mechanisms and at their different intensity. For example, the solubilization of the same amount of Fe requires more produced organic acids for biotite than for phlogopite (Balland et al., 2010). It can be hypothesized that, in view of than most rocks are not monomineralic, microorganisms are able to identify phyllosilicates that are the richest in nutrients and can be most easily decomposed and first of all attack and decompose these minerals (Fomina and Skorochod, 2020). The mineralogical composition can also affect the microbial communities of soil and the activity (biomass, dehydrogenase activity, and breathing) of communities with various species (Carson et al., 2007).

Recently acquired data indicate that deficit in mineral nutrients in an environment may stimulate the expression of specific genes that make it easier for the microbes to obtain these nutrients from clay minerals. Xiao et al. (2012) conducted experiments (although not with bacteria but with the fungus *Aspergillus fumigatus*) and have found out that the presence of K-bearing silicates at K^+ deficit increases the expression of genes facilitating the weathering of minerals and potassium leaching. These genes were responsible for the activation of enzymes (aldehyde dehydrogenase and carbonic anhydrase) that facilitate heterotrophic leaching, as well as cysteine synthase (which facilitated the enhanced production of proteins binding with metals and rich in sulfur). It has been suggested that some microorganisms acquire the ability to decompose minerals and extract nutrients from them in certain mineral media thanks to horizontal gene transfer (Xiao et al., 2012; Uroz et al., 2009). Uroz et al. (2009) acknowledged that the bacterial genus *Collimonas* had acquired the ability to efficiently weather minerals owing to mycorrhizal fungi. Thereby clay minerals themselves possess features facilitating this transfer: they are able to immobilize approaching cells and viruses on the mineral surface, adsorb DNA, and protect it prom rapid dehydration (Dröge et al., 1999).

The classic work by Stotzky (1986) postulates that the water-retentive ability of clay minerals is the most important for the origin of media favorable for bacteria, and the main resource that is attractive in soil clay minerals for microorganisms is, perhaps, water. Most natural and arable soils are, except during short periods of time after rains, snow melting, and/or irrigation, water-deficient in most of their volume for microorganisms. Among all soil particles, it is mostly clay minerals that retain large enough water amounts for supporting the growth of microbes due to the large hydrophilic surface area of these minerals. Water is retained in the pores of all phyllosilicates and in the interlayer space of clay minerals with an expandable unit cell, and can be obtained from there by bacteria. Thus, a correlation between microbial activity and the content of silt fraction in soils can result from, first of

all, the presence of water linked to this fraction but not from concentrations of nutrients and the removal of toxicants and inhibitors.

CONCLUSIONS

Interactions between bacteria and clay minerals are extremely diverse and are key factors that control the chemical composition of soils and chemical processes in them. These interactions affect both the mineralogical and the microbiological composition, as well as features of the accumulation, transformation, mobility, and biological availability of inorganic and organic compounds in soils and greatly contribute to the biogeochemical cycling of elements. Of course, not all of the processes described above are widespread in the pedosphere and biosphere, but they may occur in some environments. Obviously, the most widely spread interactions are those corresponding to the First Biogeochemical Principle formulated by V.I. Vernadsky: the biogenic migration of the atoms of chemical elements in the biosphere always tends to its maximal development.

In the absence of sufficient data and complicated methods of physicochemical analyses, V.I. Vernadsky's genius was nevertheless able to formulate several decades ago the fundamental laws and principles describing the functioning and evolution of the biosphere. These laws and principles nowadays make up the theoretical fundamentals for explaining the extremely extensive empirical data on interaction between living and inert matter. Indeed, "...his (V.I. Vernadsky's) wonderfully clever ideas will be explored and developed for decades, and many researchers should have to learn his acute, persistent, well focused, and always genial, although sometimes hard to understand, style of scientific thinking" (Fersman, 1946).

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CONFLICT OF INTEREST

The authors declare that they have no conflicts of interest.

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